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Embryonic Stages of the Patagonian Squid *Loligo gahi* (Mollusca: Cephalopoda)

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Abstract. The embryonic development of *Loligo gahi* was observed from 4-day-old eggs to natural hatching. Egg strands spawned in the Valparaíso Bay, Chile, were transported to an open system tank for incubation. Temperatures ranged from 12.9°C to 13.5°C, salinities from 34‰ to 35‰, and the photoperiod was 12L:12D. The period from spawning to hatching ranged from 30–35 days. The diameter of individual eggs ranged from 2.5–3.2 mm, and the dorsal mantle length of hatchlings varied from 2.6–3.1 mm. The pattern of chronological appearance of organs was quite similar to loliginid species previously examined (*Loligo* aff. *gahi*, *Loligo bleekeri*, *Loligo pealei*, *Loligo vulgaris reynaudii*, and *Loligo forbesii*). However, *L. gahi* had a different (faster) development time and a smaller embryo and hatchling size than *L. bleekeri* (Japan) and *L. forbesii* (eastern Atlantic Ocean). Differences (heterochronies) among species are discussed. Allometric growth of embryonic development in *L. gahi* using seven morphometric parameters was undertaken.

INTRODUCTION

Loligo gahi d'Orbigny, 1835, is a neritic cephalopod distributed along the eastern Pacific Ocean from southern Peru to southern Chile, and in the south Atlantic from the Gulf of San Matias, Argentina to Tierra del Fuego, including the Falkland Islands (Roper et al., 1984; Hatfield & Rodhouse, 1994a).

Loligo gahi is one of the target species of the international cephalopod fishery of the Falkland Islands and Argentinean waters (Hatfield, 1996). This species is also caught by trawlers and the small-scale Chilean fisheries in Pacific waters, but it is minimally commercialized in the local markets. Although several studies about the biology and ecology of *L. gahi* have been carried out (e.g., Arancibia & Robotham, 1984; Carvalho & Pitcher, 1989; Hatfield, 1991, 1996; Guerra et al., 1991; Arkhipkin, 1993; Hatfield & Rodhouse, 1994a, b), there are some important aspects of its life cycle that remain unknown. The spawning grounds of this species have not been located, and its migratory pattern is not well known.

There are about 14 species of squid in the genus *Loligo* Lamarck, 1798 (Vecchione et al., 1998). However, embryological observations have been only undertaken in *Loligo pealei* Lesueur, 1821, *Loligo vulgaris* Lamarck, 1798, *Loligo opalescens* Berry, 1911, *Loligo forbesii* Steenstrup, 1856, *Loligo bleekeri* Keferstein, 1866, and *Loligo vulgaris reynaudii* d'Orbigny, 1845 (Harman & Gardiner, 1927; Arnold, 1965; Naef, 1928; Fields, 1965; Segawa et al., 1988; Hun-Baeg et al., 1992, Blackburn et al., 1998).

Two studies on the embryonic development and the hatchling of *Loligo* aff. *gahi* (Barón, 1997a, b) based on egg masses collected from Golfo Nuevo (Argentina) in the Atlantic Ocean described the morphological changes of this species during its early stages of development. Also, Barón (1998) described morphometrics and chromatophore arrangement in the hatchlings of *Loligo* sp. from Argentinean Patagonia. However, this author indicated that the specific identity of these embryos is uncertain because both *L. gahi* and *Loligo sanpaulensis* Brakoniecki, 1984, have been reported to occur in the area.

Some authors (Nesis, 1987) maintain that the squid inhabiting the southwest Atlantic may be a different species (*Loligo patagonica* Smith, 1881). Although Brakoniecki (1986) indicated that *L. patagonica* is a junior synonym of *L. gahi*, we consider that it is necessary to undertake further morphological and genetic studies to confirm this issue.

This study shows the morphological form of the post-cleavage stages in the embryonic development of *L. gahi* from central Chile.

MATERIALS AND METHODS

The egg strings of *L. gahi* were collected from gill nets in Valparaíso Bay (33°2′S, 71°38′W, Figure 1) near the Montemar Marine Biological Station (MMBS). The nets were daily placed from 3:00 PM to 3:00 AM at 120 m depth. Twelve egg strings just spawned were carried in plastic containers with 10 L of seawater and taken to the

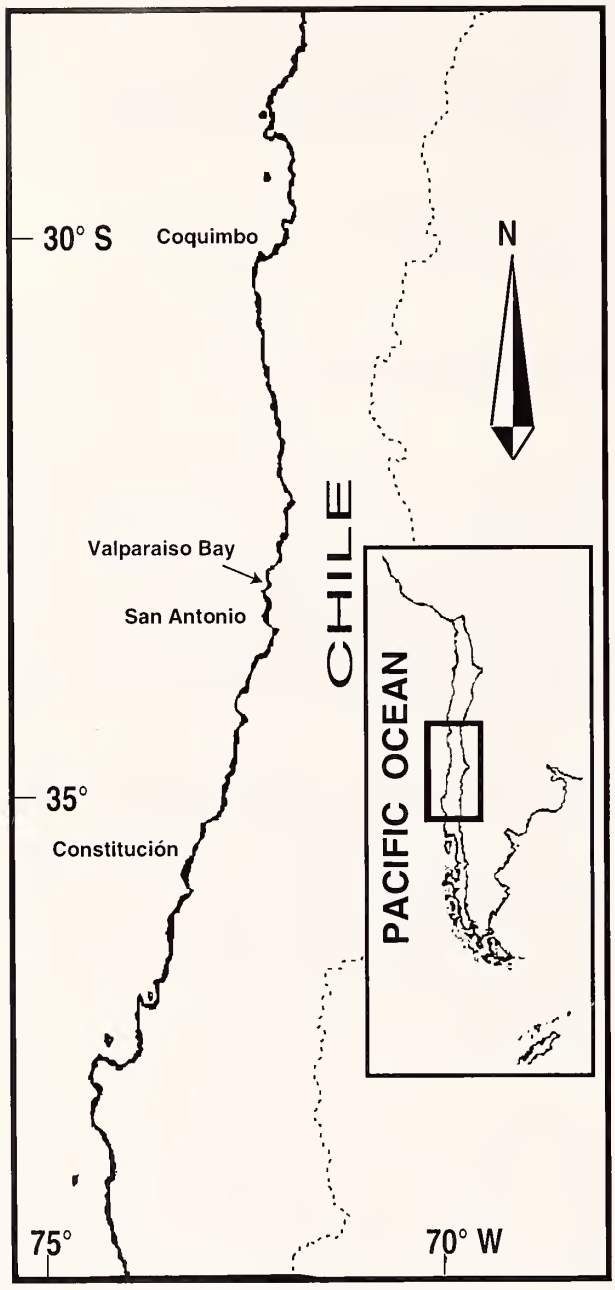

Figure 1. Location of collection of *Loligo gahi* egg masses.

open system tanks in the MMBS. The eggs were suspended in the water column and incubated at temperatures ranging from 12.9°C to 13.5°C and at salinities ranging from 34‰ to 35‰ during 35 days. The photoperiod was 12L:12D approximately. Daily observations were made from day 1 throughout the remainder of embryonic development until hatching in three egg strings with embryos of similar age. Representative living embryos were photographed daily and drawn to scale.

Table 1

Allometric growth of *Loligo gahi* during the embryonic development. ML: Mantle length in mm; HWI: Head width index; HLI: Head length index; EI: Eyeball index: MWI: Mantle width index; FLI: Fin length index: TLI: Tentacle length index. All indices are expressed as percentage of ML.

	15 days	20 days	30 days
ML	1.1	2.3	3.0
HWI	318.0	140.0	60.0
HLI	118.2	82.2	53.0
EI	86.4	41.0	23.3
MWI	181.8	104.0	90.0
FLI	63.6	48.9	40.0
TLI	86.4	48.0	46.7

The morphological staging criteria follow Arnold (1965) and they are represented in Arabic numbers. Roman numerals represent the stages proposed by Naef (1928).

Allometric growth of embryonic development was analyzed using the following morphometric indices: mantle length (ML) in mm; head width index (HWI); head length index (HLI); eyeball index (EI); mantle width index (MWI); fin length index (FLI); tentacle length index (TLI). All indices are expressed as percentages of ML.

RESULTS

The egg capsules were soft, gelatinous, and fingerlike in shape, their size ranging from 5 cm to 6 cm. Each egg capsule contained 50–60 eggs arranged in a spiral (n = 12). The size of the fresh eggs ranged from 2.5 mm to 3.2 mm in length (n = 180). The embryos hatched between 30 and 34 days, with the main hatching occurring on the 31st day. Figure 2 shows the developmental time of *L. gahi* from day 1 to hatching.

At the beginning of our observations (4 days after spawning), the eggs were at stage 13 (Arnold, 1965) or stage III–IV (Naef, 1928).

Pre-Organogenesis (Germ Layer Formation)

Day 4. Figure 3: Stage 13 (III–IV): Blastoderm covers 15–20% of the egg length. The border of the blastoderm is very distinct.

Day 5. Figure 4. Stage 14 (V): Blastoderm covers about one-half of the egg.

Day 6. Stages 15–15+ (VI–VII): Blastoderm covers about 70–75% of the egg. A shallow girdling depression appears around the equator forming a boundary between the future external yolk sac and the future embryonic body.

Table 2

Summary of egg size, development time, and hatching size in some *Loligo* species. 1, Summers (1983); 2, McMahon and Summers (1971); 3, Boletzky and Hanlon (1983); 4, Fields (1965); 5, McGowan (1954); 6, McConathy et al. (1980); 7, Barón (1997b); 8, Worms (1983); 9, Mangold-Wirz (1963); Boletzky (1974); 10, Blackburn et al. (1998); 11, Hun-Baeg et al. (1992); 12, Segawa et al. (1988).

Species	Egg size (mm)	Development time (days)	Hatchling size (mm ML)	Temperature (°C)
L. pealei	1.1–1.6[1]	10–27[2]	1.6[3]	12–23[2]
L. opalescens	2.0–2.5[4]	30–35[5]	2.5–3.2[6]	13.6[5]
L. aff. *gahi*[7]	2.6–3.1	29–33	2.6–3.2	16.0 ± 4.0
L. gahi	2.5–3.2	30–35	2.6–3.1	12.9–13.5
L. vulgaris	2.3–2.7[8]	45–70[9]	2.7[3]	12–14[9]
L. vulgaris reynaudii[10]	2.6–2.9	16–18	2.3–2.5	18.0 ± 1
L. bleekeri[11]	2.6–2.7	64–67	3.0–3.3	11.7 ± 0.4
L. forbesi[12]	3.0–3.3	68–75	4.3–4.9	12.5 ± 0.5

Organogenesis

Day 10. Figure 5: Stage 16–17 (VII): Blastoderm covers about 70–80% of egg surface. Rudimentary optic vesicle primordia are visible as a disclike elevation. The primordia of arms and tentacles become visible. The shell gland primordium is conspicuous.

Day 11. Figure 6: Stage 17 (VII–VIII): The outer yolk sac envelope is nearly closed. The optic vesicle primordia are clearly distinguishable as two thickened placodes on either side of the embryo cap. The shell gland begins to invaginate as its border elevates. The mantle primordium is first visible surrounding the shell gland.

Day 12. Figure 7: Stage 18–19 (VIII–IX): The ocular globes are protruded and covered by a membrane. The primordia of statocysts become visible. The arms and tentacles are prominent. The shell gland is practically closed and the gill primordia become visible. The anterior and posterior funnel fold primordia become visible. The optic vesicle is invaginated.

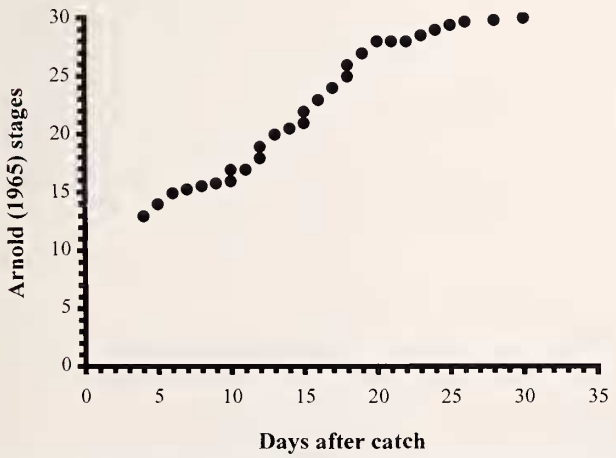

Figure 2. Embryonic development of *Loligo gahi* terms. Stages proposed by Arnold (1965) during the period from 4-day-old embryo to hatching.

Day 13. Figure 8: Stage 20 (IX): Pore of the optic vesicle closed. The anterior and posterior funnel folds extend toward the midline. The sucker primordia first appear on tentacles. Shell gland invagination progresses. Gills prominent. Fin primordia become visible.

Day 15. Stages 21–22 (X–XI): Shell gland completely closed. Mantle covers two-thirds of the gills. Lens primordia are visible for the first time. Retina pigmentation is visible, and first differentiated suckers appear on tentacles.

Day 16. Figure 9: Stage 23 (XI–XII): Fins prominent. Mantle practically covers the gills. Retina pigmentation evident and cup-shaped. Anterior and posterior funnel folds fusing together. Gills clearly segmented. Statocysts completely formed and statoliths first visible.

Day 17. Figure 10: Stage 24 (XII): Funnel tube closed. Mantle covers the gills, but funnel retractor muscle is still visible. First red chromatophores appear on arms and tentacles.

Day 18. Stages 25–26 (XIII–XIV): The mantle covers the posterior margin of the funnel completely. Tentacular clubs with 17 suckers. Buccal mass faintly visible. Posterior lobes of internal yolk sac increase in size, but external yolk sac still longer than embryonic body. Ink sac becomes visible, but no ink is present. First chromatophores present in the surface of dorsal mantle.

Day 19. Figure 11: Stages 27 and 27+ (XVI–XVII): Hoyle's organ evident on posterior dorsal mantle between fins. Buccal mass and esophagus clearly visible. External yolk sac still slightly longer than embryonic body.

The buccal mass in embryos of *L. gahi* appears earlier than suggested by Figure 11 and the descriptions for stages 25–26 (XIII–XIV), but its formation can only be observed clearly from the dorsal side, which is not represented in the figures.

Days 20–21–22. Stage 28 (XVIII): Chromatophores clearly present on dorsal and ventral mantle, ventral and dorsal head, arms, and tentacles. Four chromatophores on tentacle. Internal yolk sac approximately same size as mantle length. Primary lid covers the optic vesicle completely, and part of it is transformed into a cornea.

Days 24–25–26. Figure 12. Stages 29−29+−29++ (XIX−XIX+−XX): External yolk sac smaller than embryonic body and becoming progressively depleted. Anus and anal flaps are conspicuous and clearly visible. Posterior lobes of internal yolk sac forming small round bodies in the posterior part of the mantle. Four red chromatophores on each tentacle interspersed with three or four yellow ones. Stomach and caecum clearly visible. Ink sac filled with ink. At the end of these observations, mid-gut gland is clearly visible. Internal yolk sac much reduced in size.

Days 30–31. Figures 13, 14. Stage 30 (XX): Hatching. Remaining external yolk sac dropped. Hoyle's organ depleted. Posterior lobes of internal yolk sac reduced to small round bodies. The number of ventral mantle chromatophores ranged from 40–58; the yellow ones were grouped in pairs, whereas the red ones were distributed in a more or less regular grid of oblique imaginary lines. The number of red chromatophores on the ventral side of the head ranged from 38 to 42. There were three to four red chromatophores on the right and left sides of each cheek. Four brown chromatophores were observed in the center of the dorsal side of the mantle, surrounded by eight yellow chromatophores located in the margins of the mantle. One hexagon of six brown chromatophores was found on the dorsal side of the head. Hatching size ranged from 2.6–3.1 mm ML (n = 60). Arm formula: III > IV = II > I.

Table 1 shows the allometric growth of the embryo based on the comparison between several morphometric indices measured at days 15, 20, and 30.

Based on the observed sequence of development of the major embryonic features, the developmental pattern of *L. gahi* was compared to that of *L. pealei*, *L. forbesii*, *L. bleekeri*, *L.* aff. *gahi*, and *L. vulgaris reynaudii* (Arnold, 1965; Segawa et al., 1988; Hun-Baeg et al., 1992; Barón, 1997b; Blackburn et al., 1998). The results of the comparisons are shown in Figure 15. *L. gahi* showed (Table 2) a different (faster) development time and a smaller embryo and hatching size than *L. bleckeri* (Japan) and *L. forbesii* (eastern Atlantic Ocean).

DISCUSSION

The eggs of *L. gahi* developed rapidly from stage 1 to stage 10 during the first five days after spawning. Formation of the germ layer (gastrulation) is a complex process that begins when the margin of the blastoderm becomes two-layered as described in *L. pealei*, *L. vulgaris*, *L. forbesii*, and *L. bleekeri* (Singley, 1977; Marthy, 1982; Segawa et al., 1988; Hun-Baeg et al., 1992). The definitive separation of the blastoderm into an ectodermal and a mesodermal germ layer is accomplished during stages 12 and 13 (III). Thereafter, the developmental pattern of the eggs became linear with a gentle slope (Figure 2). This developmental pattern in *L. gahi* was similar to that observed in *L. pealei* and *L. bleekeri* (Arnold, 1965; Hun-Baeg et al., 1992). However, Segawa et al. (1988) found a sigmoid curve in the internal organogenesis of *L. forbesii*.

As shown in Table 2, at a similar range of temperature, the average development time and mantle lengths of loliginid hatchlings seem to be inversely related to the egg size. Furthermore, egg diameter in other species ranges in size from 1.0–3.3 mm. Therefore, *L. gahi* has relatively large eggs (2.5–3.2 mm). Hatchlings of *L. gahi* are of medium size. They are smaller than *L. bleekeri* and *L. forbesii* and larger than *L. pealei* (Table 2). Same species-specific differences may exist in the first appearance of the organs. At present, the embryonic development using living embryos is suitable for comparison of six *Loligo* species (*L. gahi*, *L.* aff. *gahi*, *L. bleekeri*, *L. pealei*, *L. vulgaris reynaudii*, and *L. forbesii*). Naef (1928) described the embryological development of *L. vulgaris*, but based on preserved embryos instead of living animals. Fields (1965) described the embryological development of *L. opalescens*, but related the development to daily growth rather than to a staging system that could be applied over a range of temperatures and development rates.

The pattern of chronological appearance of organs is quite similar in the loliginid species examined so far. However, several differences are evident among these species (Figure 15). The primordium of the shell gland (PSG) appears in *L. bleekeri*, *L.* aff. *gahi*, and *L. gahi*

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Figures 3 to 14. Ventral view of embryonic development of *Loligo gahi*, from stage 13 of Arnold (1965) to newly hatched squid. See Results for details of each figure. Key to abbreviations: aliys, anterior lobe inner of the yolk sac; ap, anal papilla or flaps; bd, blastoderm; bh, brachial heart; bu, buccal mass; ch, chorion; f, funnel; g, gill; ho, Hoyle's organ; is, ink sac; m, mantle; o, optic vesicle; pa, primordia of arms; paf, primordia of anterior funnel fold; pf, primordia of fins; pg, primordia of gill; pl, primordia of lens; pliys, posterior lobes inner of the yolk sac; pm, primordia of mantle; po, primordia of optic vesicle; ppf, primordia of posterior funnel fold; ps, primordia of suckers; psg, primordia of shell gland; pst, primordia of statocysts; r, retina; sg, shell gland; st, statocysts; su, sucker; yo, yolk. Scale bar: 1 mm.

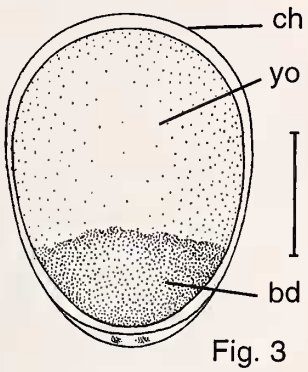


Fig. 3

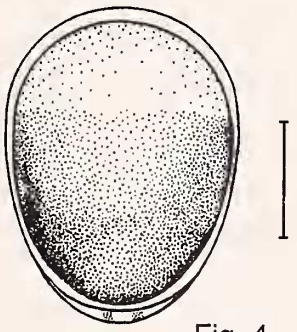
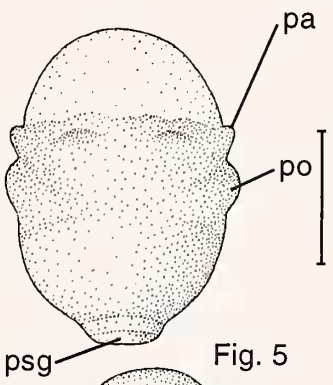


Fig. 4



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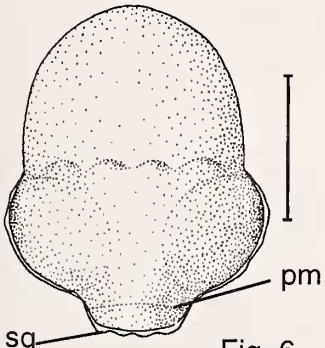

Fig. 6

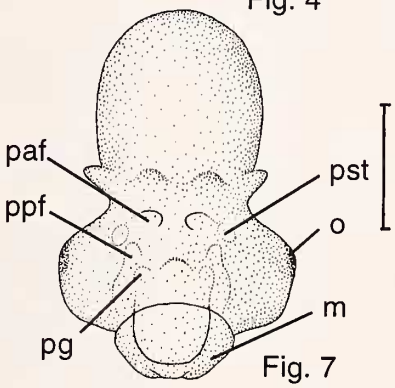

Fig. 7

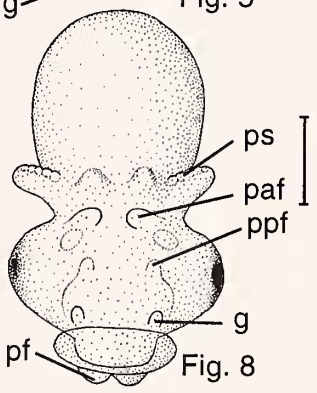

Fig. 8

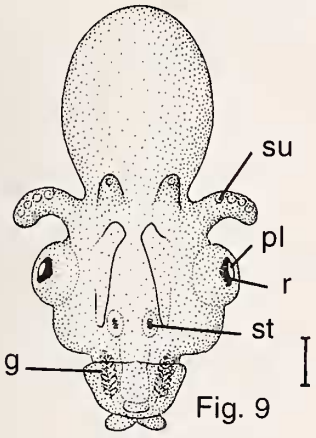

Fig. 9

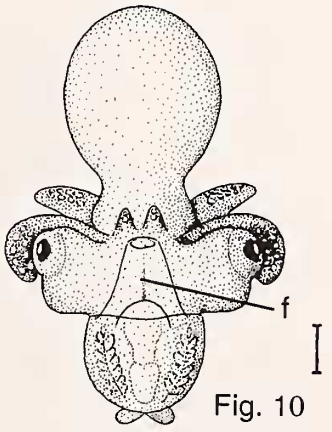

Fig. 10

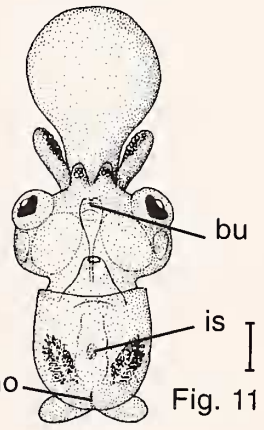

Fig. 11

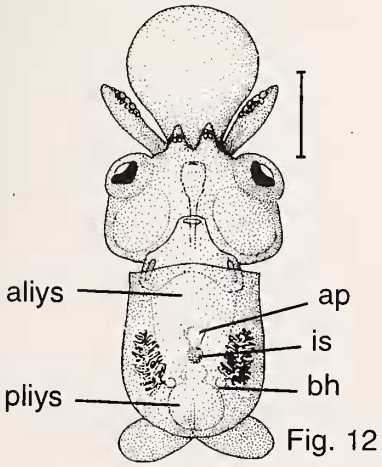

Fig. 12


Fig. 13


Fig. 14

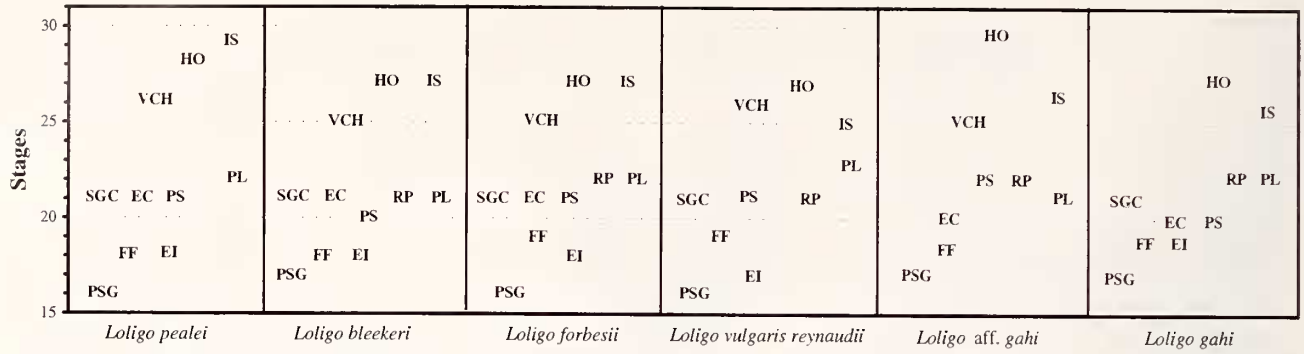

Figure 15. Comparison of chronological appearance of select organs in six species of the genus *Loligo*, using Arnold's (1965) stage system. Key to abbreviations: EC, eye vesicle closed; EI, eye vesicle invagination begins; FF, funnel formation begins; HO, Hoyle's organ appears; IS, ink sac appears; PL, primordia of lens visible; PS, primordia of suckers appear; PSG, primordia of shell gland appears; RP, retina pigmentation begins; SGC, shell gland closed; VCH: ventral mantle chromatophores appear.

later (stage 17) than in *L. vulgaris reynaudii*, *L. pealei*, and *L. forbesii* (stage 16). Funnel formation starts in stage 18 in all loliginid species examined except in *L. vulgaris reynaudii* and in *L. forbesii* (stage 19). Eye vesicle invagination begins to occur in *L. gahi* in stage 19, whereas it occurs in stage 18 in *L. pealei*, *L. bleekeri*, and *L. forbesii*. Barón (1997b) gives no information on when this change occurs in *Loligo* aff. *gahi*. Closure of the eye vesicle occurs in both *L. gahi* and *L.* aff. *gahi* during stage 20, whereas it occurs during stage 21 in the other species. Appearance of the primordia of suckers (PS) on the tentacles was observed in stage 20 for *Loligo gahi* and *L. bleekeri*, and in stage 21 for *L. pealei* and *L. forbesii*. Barón (1997a) and Blackburn et al. (1998) observed the appearance of primordia of suckers in stage 22 in *L.* aff. *gahi* and *L. vulgaris reinaudii*, respectively. Retina pigmentation appears in *L. gahi* later (stage 22) than in the other loliginid species. This, however, could be due to the lack of suitable observations in these species as was the case with the primordium of lens. Ink sac (IS) appearance occurred in *L. gahi* and *L.* aff. *gahi* earlier (stage 26) than in the other three species previously analyzed (stages 27–29), except in *L. vulgaris reynaudii* where it occurred in stage 25. Hoyle's organ (HO) was observed in *L. gahi*, *L. vulgaris reynaudii*, *L. forbesii*, and *L. bleekeri* in stage 27, but it occurs in stage 29 in *L. pealei*. Barón (1997b) indicated that this form is visible in stage 29–30. In all cases, differences among species were restricted within a narrow range of no more than three stages. All of the above-mentioned differences might be due to different observation techniques or rearing conditions (temperature, oxygen concentration, salinity, etc.) rather than heterochronies, as discussed by Boletzky (1987). Although all congeneric species we compared our results with were studied using living embryos, not all of them were maintained under the same conditions.

The chromatophore pattern and size of newly hatched *L. gahi* were quite similar to that observed in *L.* aff. *gahi* and *Loligo* sp. (Barón, 1997a; 1998).

Brakoniecki (1986) placed all of the American *Loligo* species (e.g., *L. gahi*, *L. opalescens*, *L. pealei*, and *L. plei*) in a separate genus, *Doryteuthis* Naef, 1912, because of several distinct morphological characteristics of the hectocotylus. This author considered that *L. bleekeri* and *L. pealei*, placed by Natsukari (1984) within the genus *Heteroteuthis*, could be a junior synonym of *Doryteuthis*. Comparison of organogenesis of *Doryteuthis* and *L. forbesii* revealed no differences between these species. Similar linear curves of internal organogenesis have been observed in all *Doryteuthis* species. However, these curves are different from the sigmoid curve found by Segawa et al. (1988) in the organogenesis of *L. forbesii*.

Hunter & Simon (1975) previously reported on the extreme homogeneity observed in the morphological development of loliginid squids. Indeed, this homogeneity does not allow one to determine whether the embryonic development described by Barón (1997b) belongs to *L. gahi*, although the similarity of the chromatophore pattern in newly hatched specimens suggests that both might be the same species. However, further comparative studies are necessary to elucidate this issue.

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